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DIVERSITY AND HABITAT DIFFERENTIATION OF MOSSES AND LIVERWORTS IN THE CLOUD FOREST OF MONTEVERDE, COSTA RICA

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ABSTRACT

An inventory of the understory and canopy of 4 ha of lower montane cloud forest at Monteverde, Costa Rica, yielded 190 bryophyte species: 133 hepatics, 56 mosses and 1 hornwort. Thick branches of the lower canopy were by far the richest habitat in terms of number of species (99), trunks from 1 m upwards had 65 species, lianas, shrubs, saplings, or living leaves in the understory had about 36-46 species each, and 16 species were found on rotten logs. The figures are illustrative of the great diversification of microhabitats of bryophytes in a tropical montane cloud forest. About 36% of the species, including more than half of the corticolous ones, occurred exclusively in the canopy. It appeared that the percentage of bryophyte species restricted to the canopy may be the same in lowland and montane rain forests, in spite of the great differences in species abundance and composition in the two kinds of forest.

Key words. Bryophytes, Cloud forest, Biodiversity, Costa Rica.

RESUMEN

Ciento noventa especies de briofitas (133 hepáticas, 56 musgos, 1 antocerote) fueron encontradas en un inventario hecho en 4 hectáreas del sotobosque y el dosel en el bosque nublado (1500 m) de Monteverde, Costa Rica. Las ramas gruesas del dosel fueron la porción más rica en termino de numero de especies (99), en troncos había 65 especies, lianas, arbustos, árboles juveniles o hojas vivas en el sotobosque tenían entre 36-46 especies cada una, y 16 especies fueron encontradas en troncos en descomposición. Las cifras ilustran la gran diversidad de microhabitats de briofitas en el bosque nublado. Cerca de 36% de las especies, incluyendo mas de la mitad de los corticolos, se presentaron exclusivamente en el dosel. Parece que el porcentaje de especies de briofitas restringidas al dosel podría ser el mismo en bosques de tierras bajas y en bosques nublados, a pesar de la gran diferencia en abundancia y composición taxonómica de las briofitas en las dos clases de bosque.

Palabras clave. Briofitas, Bosque nublado, Biodiversidad, Costa Rica.

INTRODUCTION

Tropical rain forests, including montane cloud forests, harbour a large diversity of bryophytes, probably due to the great variety of microhabitats in these forests. Of an estimated 4000 species (2650 mosses, 1350 hepatics) occurring in tropical America, about 80% of the hepatics and 50 % of the mosses are confined to these forests (Gradstein et al., in press). Most of the bryophytes in tropical rain forest are epiphytes and their abundance varies considerably with elevation. In lowland rain forests, below 500 m, bryophyte cover is poor and mostly restricted to the canopy. In montane rain forests, especially in the very moist cloud forests, growth of epiphytic bryophytes is usually much more luxuriant. Moreover, the forest floor may be covered with dense bryophyte carpets. The lower temperatures and higher light levels in the cloud forest and the availability of plentiful water due to impact of fog favour the accumulation of dead organic material on the ground and the abundant growth of the epiphytic and terrestrial bryophytes (Richards, 1984; Gradstein & Pócs, 1989).

Our understanding of bryophyte diversity of tropical rain forests is still fragmentary. Complete inventories are very scarce. Most studies only deal with part of the flora, leaving "difficult" groups such as the tiny Lejeuneaceae (Hepaticae) unidentified. Moreover, attention is usually restricted to the lower part of the forest, whilst the higher portions of the trunks and the canopy branches are neglected due to their inaccessibility (Wolf, 1993). Cornelissen and Gradstein (1990) found that in lowland rain forest of Guyana about 50 % of the bryophyte species occurred only in the tree crowns and on the upper portions of the trunks, over 10 m above ground level. In contrast, only 14 % of the species were exclusive to the understory. The number of species restricted to the canopy in cloud forests is still unknown. Another important finding of recent work is that species density of epiphytic bryophytes in rain forests is high and minimum areas for sampling therefore relatively small. Complete sampling of 4-5 trees (from base to outer canopy) may yield over 75% of the flora of a homogeneous forest stand (Cornelissen & ter Steege, 1989; Wolf, 1993; Gradstein et al., 1996). Costa Rica's Monteverde Cloud Forest Reserve is one the best studied montane moist forests worldwide. *Monteverde: Ecology and Conservation of a Tropical Cloud Forest* (Nadkarni & Wheelwright, 1999) incorporates contributions of 140 authors and over 1800 references. Vascular epipyhtes have been studied in detail by Nadkarni and associates (e.g., Nadkarni, 1986; Nadkarni & Matelson, 1992; Ingram & Nadkarni, 1993). In contrast, very little work has been done on the bryophytes of Monteverde. Reed & Robinson (1971) published a first list of 164 species (90 mosses, 73 hepatics, 1 hornwort) based on random collecting in the forests and in pasture areas. Additional species were reported by Gradstein et al. (1994) and Sillet et al. (1995). The latter authors analysed the epiphytic bryophyte flora in the canopy of six *Ficus tuerckheimii* trees, three in the dense primary forest and three isolated ones in adjacent pasture land, and could demonstrate that the two sets of trees had very different species assemblages.

This paper deals with the bryophyte diversity in the cloud forest of Monteverde. The main purpose of this study was to described the composition and habitat differentiation of the flora and to determine floristic differences between the canopy and understory of the forest.

MATERIAL AND METHODS

We conducted an inventory of bryophytes within a 4 ha study site, consisting of four plots of one hectare each, in Monteverde Cloud Forest Reserve during November 1992 and January 1994. The Monteverde Cloud

Forest Reserve is situated in northcentral Costa Rica (10°18'N, 84°48'W) along the crest of the continental divide in the Cordillera de Tilarán. The forest is subject to cloud-bearing trade winds that move across the Cordillera from the northeast. The trade winds occur throughout the year, but most frequently deliver mist between November and May. Total annual annual rainfall is 2000-2500 mm, most of which falls during May to October, but fog and mist may contribute an additional 500-2000 mm of annual precipitation (Ingram & Nadkarni, 1993).

The 4 ha study site is in the lower montane rain forest (1550 m elevation) about 1 km southwest of the headquarters of the reserve, on the leeward, Pacific side of the Cordillera. The primary forest is 20-30 m high with a few emérgents to 35 m tall. *Ocotea tonduzii* (Lauraceae), *Ficus tuerckheimii* (Moraceae) and *Meliosma ideapoda* (Sabiaceae) are the principal canopy tree species, making up ca. 40% of total basal area of trees.

About 350 collections of bryophytes were gathered randomly in the four hectare plots. An average of 2-3 trees per plot were climbed and samples were taken from branches of the lower canopy. Sampling of the outer canopy was done from recently fallen trees. In general, canopy sampling was less detailed than the inventory of the understory, however. The collections were deposited in FLAS, U and USJ.

RESULTS AND DISCUSSION

1. ***Distribution of species in the cloud forest.*** Bryophytes were abundant on treelets, shrubs, lianas and rather exposed trunks in the forest understory and, particularly, on thick branches of the inner forest canopy. On trunks in deep shade, bryophyte cover was usually rather scanty. Hepatics were more abundant than mosses, both in terms of biomass and in number of species.

Understory. The bryophyte flora of the forest understory was very different from that of the canopy. The most frequent bryophytes on trunks, shrubs, lianas etc. in the understory were *Plagiochila spp.*, *Porotrichum korthalsianum* and *Radula antillana.* Other common taxa included *Metzgeria leptoneura*, *Lepidopilum muelleri*, *Omphalanthus filiformis*, *Taxilejeunea pterigonia* and *Trichocolea tomentosa.* In well-lit sites the pendent mosses *Phyllogonium fulgens* and various *Meteroriaceae* were frequently seen together with the robust hepatics *Porella swartziana*, *Bryopteris filicina*, *Radula gottscheana* and *Plagiochila spp.*

On trunk bases *Cephalozia crassifolia*, *Fissidens* spp., *Hookeriopsis falcata*, *Hypopterygium tamariscimum*, *Lophocolea connata*, *Telaranea nematodes* and various unidentified species of *Lejeunea* were quite common. Other taxa characteristic of this habitat included *Calypogeia* spp., *Pallavicinia lyellii*, *Cyrtohypnum schistocalyx* (= *Thuidium schistocalyx*), *Leskeodon andicola*, *Octoblepharum erectifolium* and *Syrrhopodon* spp. Species of *Bazzania* occurred here and there on trunk bases but were much more common in the forest canopy.

The forest floor had much rotten wood (logs, fallen branches) and this was also an important habitat for bryophytes, e.g., the thalloid hepatics *Monoclea gottschei* and *Riccardia spp.* and the mosses *Hookeriopsis falcata*, *Mittenothamnium reptans*, *Plagiomnium rhynchophorum* and *Pyrrhobryum spiniforme.* The single hornwort encountered in the study site, *Megaceros vincentianus*, was also a species of rotten logs. The majority of the species of rotten logs also occurred on the trunk bases, especially on rotten, humose ones.

Canopy. The lower, ± horizontal branches of the canopy were thickly covered by bryophyte mats. Species of *Bazzania*, *Lepidozia, Macromitrium, Plagiochila*, *Herbertus* and *Frullania convoluta* were the most prominent elements. *Macromitrium* and *Herbertus* were restricted to the canopy but species of *Bazzania* and *Lepidozia* also occurred lower down in the understory. Plants of *Frullania convoluta* fallen from the canopy sometimes continued growth on branches in the understory.

Other bryophytes characteristic of thick canopy branches and lacking in the understory included the hepatic genera *Frullania, Adelanthus* and *Ceratolejeunea* (the latter sometimes forming extensive dark mats), furthermore *Kurzia capillaris, Leptoscyphus porphyrius, Syzygiella pectiniformis*, *Tylimanthus laxus*, and the mosses *Acroporium pungens, Bryum capillare*, *Campylopus arctocarpus*, *Leucobryum giganteum*, *Leucoloma cruegerianum*, *Pilotrichella flexilis, Squamidium nigricans*, and *Syrrhopodon lycopodiodes*. Light-green mats of *Papillaria imponderosa* and the pendent *Phyllogonium*s and *Omphalanthus filiformis* were common both in the canopy and in the understory, behaving as ecological "generalists".

Fine twigs of the outer canopy harboured a rich ramicolous bryophyte community characterized by *Daltonia gracilis* and many small species of *Lejeuneaceae*. Some of these also grew on living leaves. Foliicolous bryophytes, most of them *Lejeuneaceae*, were abundant especially in the forest understory. The most common ones included *Odontolejeunea lunulata* and species of *Cyclolejeunea (C. convexistipa, C. peruviana), Drepano-lejeunea* and *Aphanolejeunea.*

2. ***Species richness***. Our inventory yielded 190 bryophyte species (Table 1): 133 hepatics, 56 mosses, and 1 hornwort *(Megaceros vincentianus*). The average number per hectare was 88 species, with highest number in plot 2 (118) and lowest number in plot 4 (74). In comparison, a very detailed analysis of the canopy by Sillet et al (1995) found 109 bryophyte species on three *Ficus tuerckheimii* trees in the Monteverde cloud forest. This suggests that our canopy species list is still incomplete.

Species-area curves showed that one plot yielded 45 % of total diversity, and two plots yielded 75% (Fig. 1). In comparison, when bryophyte diversity on trees only is studied (excluding shrubs, logs etc.), the 75% level is usually obtained by analysis of just four trees (Wolf, 1993).

The absolute dominance of hepatics over mosses at the study site in terms of species number is characteristic of these neotropical moist forests. In palaeotropical forest, mosses tend to be more abundant (Gradstein & Pócs, 1989). *Plagiochila* was by far the most

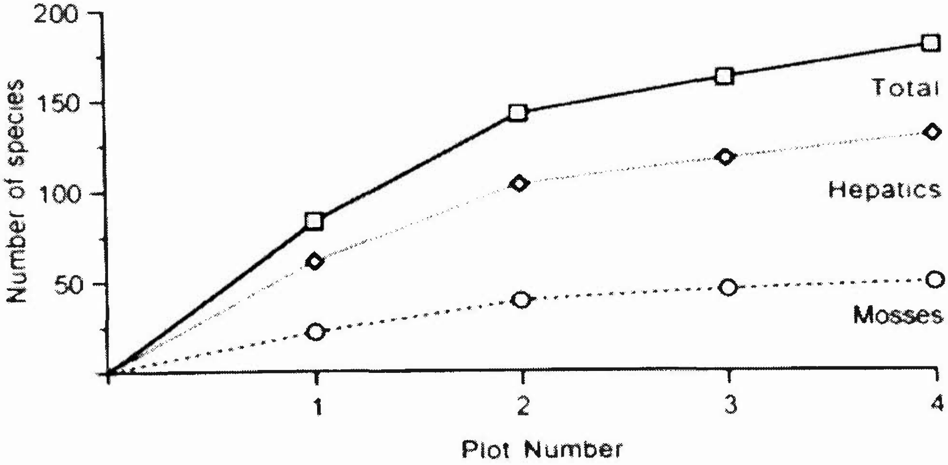

Fig. 1. Species-plot relationships.

speciose genus (18 spp.), followed by the hepatic genera *Lejeunea* and *Bazzania* (7 spp. each), and *Frullania* and *Radula* (6 spp.). Among the mosses, *Lepidopilum* and *Macromitrium* (4 spp.) were the most speciose genera, the former mainly in the understory, the latter very abundant in the canopy.

3. ***Habitat diversification***. The distribution of the species of the species over the various microhabitats is shown in Fig. 2. Thick branches of the lower canopy were by far the richest habitat for bryophytes and yielded about 100 species. Trunks (from 1 m upwards) had 65 species, living leaves 46 species and trunk bases 36 species. Fourty species were found on lianas, poles and small branches on shrubs, sapling etc. in the forest understory. The lowest number of species (17) was found on rotten logs; however, half of these were exclusive to rotten logs and not found elsewhere. A similar percentage was obtained for epiphylls: about half of the foliicolous species (23) were only found on living leaves, others occurred also on other substrates. The figures are illustrative of the great diversification of microhabitats of bryophytes in a tropical montane forest.

Species richness in the canopy compared to the understory was 117 vs. 121. Of these, 48 (25%) occurred both in the canopy and the understory, 38% were exclusive to the understory, and 36% to the canopy (Fig. 3A).

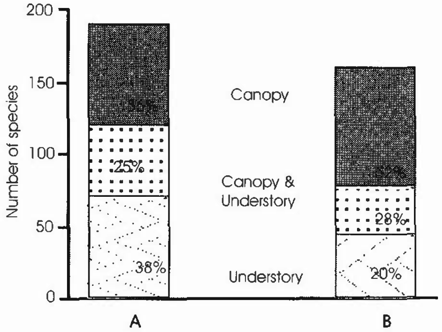

Fig. 3. Comparison of bryophyte species richness in understory and canopy. A. Total species diversity. B. Corticolous species diversity (species of rotten logs and epiphylls excluded).

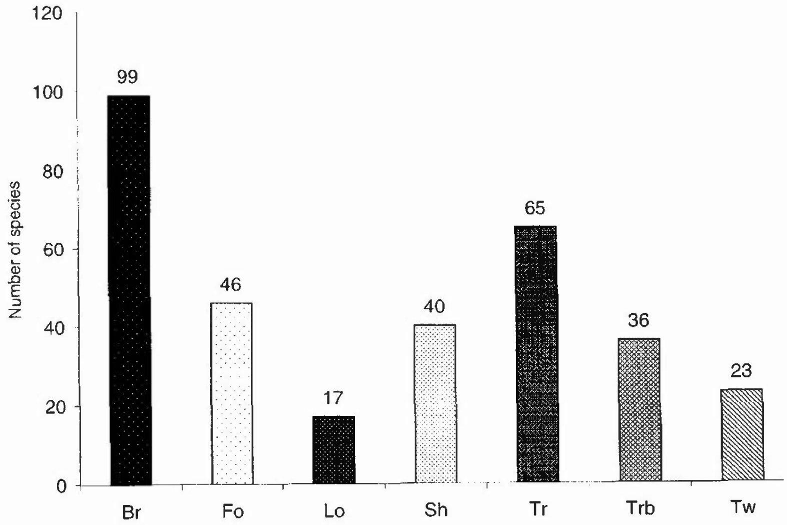

Fig. 2. Distribution of bryophyte species over different microhabitats. For abbreviations see Table 1.

Table 1. Bryophyte species collected in the 4 ha study site (hectare plots 1-4) in the Monteverde Cloud Forest Reserve.

	PLOT	CANOPY	UNDERSTORY
HEPATICAE			
Acrobolbaceae			
Tylimanthus laxus Spruce	1, 2, 4	Br	-
Adelanthaceae			
Adelanthus carabayensis (Mont.) Grolle	1	Br	-
A. decipiens (Hook.) Mitt.	2	Br	-
A. pittieri (Steph.) Grolle	4	Br	-
Aneuraceae			
Riccardia fucoidea (Sw.) Schiffn.	4	Br	Lo
R. sp.	1, 2, 3, 4	Br	Lo
Calypogeiaceae			
Calypogeia crenulata Bischler	1	-	Trb
C. peruviana (Nees & Mont.) Steph.	3	-	Trb
C. rhombifolia (Spruce) Steph.	3	-	Trb
C. rhynchophylla (Herz.) Bischler	2	-	Trb
Cephaloziaceae			
Cephalozia crassifolia (Lindenb. & Gott.) Fulf.	1, 2, 3, 4	Br	Lo, Sh, Trb
Odontoschisma longiflorum (Tayl.) Steph.	4	Br	-
Geocalycaceae			
Leptoscyphus porphyrius (Nees) Grolle	2	Br	-
Lophocolea connata (Sw.) Nees	1, 2, 3, 4	-	Lo, Trb
L. muricata (Lehm.) Nees	2, 3, 4	-	Fo, Sh, Tr, Trb
L. trapezoidea Mont.	2	Br	-
Herbertaceae			
Herbertus divergens Steph.	1	Br	-
H. juniperoideus (Sw.) Grolle	?	Br	-
H. pensilis Tayl.	1, 2, 4	Br	-
Jubulaceae			
Frullania arecae (Spreng.) Gott.	2	Br	-
F. brasiliensis Raddi	2, 4	Br	-
F. convoluta Lindenb. & Hampe	1, 2, 3, 4	Br	Sh (fallen from canopy?)
F. exilis Tayl.	1, 2, 4	Br, Tw	-
F. laxiflora Spruce	2	Br	-
F. riojaneirensis (Raddi) Aongstr.	2	Br	-
Jubula bogotensis Gott.	3	-	Tr
Jungermanniaceae			
Syzygiella pectiniformis Spruce (det. Vána)	2	Br	-
Lejeuneaceae			
Anoplolejeunea conferta (Meissn.) Schiffn.	?	Br	-
Aphanolejeunea exigua Evans	2, 4		Fo
A. gracilis Jov.-Ast	1, 2, 3, 4		Fo
A. subdiaphana var. cristulata (Schust.) Pócs	1, 2, 3, 4		Fo
Brachiolejeunea laxifolia (Tayl.) Schiffn.	2	Tw	-
Bryopteris filicina (Sw.) Nees	1, 2, 4	Br	Sh, Tr
Ceratolejeunea cornuta (Lindenb.) Steph.	2	Br	-
C. maritima (Spruce) Steph.	1, 2, 4	Br	Fo
C. sp.	1, 2	Br	-
Cheilolejeunea rigidula (Mont.) Schust.	1, 2	Br	-
Cololejeunea cf. standleyi Herz.	1, 2, 3, 4		Fo
Colura ulei Jov.-Ast	2	Tw	-
Cyclolejeunea accedens (Gott.) Evans	2, 3, 4	-	Fo
C. convexistipa (Lehm. & Lindenb.) Evans	1, 2, 3, 4	Fo	Fo
C. luteola (Spruce) Grolle	4		Fo
C. peruviana (Lehm. & Lindenb.) Evans	1, 2, 3, 4	Fo, Tw	Fo
Dicranolejeunea axillaris (Nees & Mont.) Schiffn.	2	Tw	-
Diplasiolejeunea alata Jov.-Ast	2	Tw	-
D. brunnea Steph.	3		Fo
D. cavifolia Steph.	2, 3	Tw	Fo
D. johnsonii Evans	1, 4	Br	Fo
D. montecristensis Winkler	3		Fo
D. pellucida (Meissn. ex Spreng.) Schiffn.	1, 2, 3, 4	Tw	Fo
Drepanolejeunea campanulata (Spruce) Steph.	1		Fo
D. inchoata (Meissn.) Evans	1, 2, 3	Br, Tw	Fo
D. lichenicola (Spruce) Steph.	2	Tw	-
Echinocolea dilatata (Evans) Schust.	3, 4		Fo
Harpalejeunea aspera Grolle	3		Fo
H. oxyphylla (Nees & Mont.) Steph.	4		Fo
Lejeunea cephalandra Spruce	2	Br	
L. controversa Gott.	1, 2, 4		Lo, Sh, Tr, Trb
L. aff. filipes Spruce	1, 2	Tw	-
L. flava (Sw.) Nees	1, 2	Br	Tr
L. phyllobola Nees & Mont.	2	Tw	-

Conventions

Br = thick, ± horizontal branches of the inner forest canopy
Fo = living leaves (foliicolous)
Lo = rotten logs
Sh = lianas, poles and small branches (of shrubs, treelets and saplings) in the forest understory
Tr = tree trunks (from 1 m upwards)
Trb = bases of tree trunks (0-1 m) and roots
Tw = twigs of the outer forest canopy

Cont. Table 1

	PLOT	CANOPY	UNDERSTORY
L. (subgen. Otigoniolejeunea) sp.	2, 3	-	Sh, Trb
L. sp. A	2, 3	-	Sh
L. sp. B	1, 3	-	Tr, Trb
Lepidolejeunea involuta (Gott.) Grolle	1, 2	Br	Fo, Tr
Leptolejeunea elliptica (Lehm. & Lindenb.) Schiffn.	2, 3		Fo
L. serratifolia Schiffn.	1, 2		Fo
Macrolejeunea lancifolia (Steph.) Herz.	1, 2, 3, 4	-	Fo, Sh
Marchesinia robusta (Mitt.) Schiffn.	4	Br	-
Microlejeunea acutifolia Steph.	3		Fo
M. bullata (Tayl.) Evans	1, 2, 3	Tw	Fo
M. stricta (Gott. et al.) Steph.	1, 4		Fo
Neurolejeunea breutelii (Gott.) Evans	2	Br	-
Odontolejeunea decemdentata (Spruce) Steph.	2, 3		Fo
O. lunulata (Web.) Schiffn.	1, 2, 3, 4	Fo, Tw	Fo
Omphalanthus filiformis (Sw.) Nees	1, 2, 3, 4	Br, Tw	Fo, Sh
O. grandistipulus Steph.	2, 4	Br	-
O. ovalis (Lindenb. & Gott.) Gradst.	1, 2, 4	Br	Fo, Sh
Prionolejeunea schlimiana (Gott.) Steph. (det. Grolle)	1, 3	-	Fo, Sh
P. sp.	1, 2	-	Fo, Sh
Rectolejeunea berteroana (Gott.) Evans	2, 3, 4	Tw	Fo
Stictolejeunea squamata (Willd. ex Web.) Schiffn.	1, 2		Fo
Symbiezidium transversale (Sw.) Trevis. var. hookerianum (Gott. et al.) Gradst. & van Beek	3	Br	-
Taxilejeunea sulphurea (Lehm. & Lindenb.) Schiffn.	3	-	Fo, Sh
T. pterigonia (Lehm. & Lindenb.) Schiffn.	2, 3, 4	Br	Sh
T. sp.	4	-	Lo
Lepidoziaceae			
Bazzania affinis (Lindenb. & Gott.) Trevis.	1, 2, 3, 4	Br	Tr, Trb
B. breuteliana (Lindenb. & Gott.) Trevis.	2	Br	Trb
B. denticulata (Lindenb. & Gott.) Trevis.	4	Br	-
B. gracilis (Hampe & Gott.) Steph.	1, 4	Br	Trb
B. hookeri (Lindenb.) Trevis.	2, 3, 4	Br	Trb (rare)
B. longa (Nees) Trevis.	1	Br, Tr	Tr
B. stolonifera (Sw.) Trevis.	?	Br	-
Kurzia capillaris (Sw.) Grolle	1	Br	Fo
Lepidozia armata Steph.	4	Br	-
L. cupressina (Sw.) Lindenb.	1, 2	Br, Tr	TRb
L. squarrosa Steph.	4	Br	-
Telaranea nematodes (Gott. ex Aust.) Howe	1, 2, 3, 4	-	Lo, Trb
Metzgeriaceae			
Metzgeria albinea Spruce	2	Br	-
Metzgeria decipiens (Mass.) Schiffn.	1, 2, 3,	-	Fo, Sh, Tr
M. leptoneura Spruce	2, 3, 4	-	Sh
M. liebmanniana Lindenb. & Gott.	2	Tw	-
Monocleaceae			
Monoclea gottschei Lindb.	1, 2, 3, 4	-	Lo, Trb
Pallaviciniaceae			
Pallavicinia lyellii Hook.	1, 2	Br	Trb
Symphyogyna brogniartii Mont.	4	-	Lo
Plagiochilaceae			
Plagiochila adiantoides (Sw.) Lindenb.	2, 3, 4	Br	Sh
P. aerea Tayl.	1, 2, 4	Br	-
P. breuteliana Lindenb.	1, 2, 3, 4	-	Trb
P. crispabilis Lindenb.	3	-	Sh
P. cristata (Sw.) Lindenb.	1, 4	Br	-
P. diversifolia Lindenb. & Gott.	2, 3	-	Sh, Tr
P. gymnocalycina (Lehm. & Lindenb.) Mont.	2	Br	Sh
P. laxa Lehm. & Lindenb.	1, 2, 3	Br	Sh, Tr, Trb
P. martiana Nees	2	-	Sh
P. miqueliana Lehm. & Lindenb.	2, 4	Br	-
P. raddiana Lindenb. (= P. guilleminiana Nees & Mont.)	4	Br	Tr
P. rudischusteri Robins.	4	-	Sh
P. stolonifera Lindenb. & Gott.	2	Br	-
P. stricta Lindenb.	1, 2	Br	Trb
P. subplana Lindenb.	1, 2	Br	-
P. tenuis Lindenb.	2, 3, 4	Tw	Tw, Sh (rare)
P. sp. A	1, 2	Br	-
P. sp. B	1, 2	Br	-
Porellaceae			
Porella swartziana (Web.) Trevis.	1, 2, 3,	Br	Sh, Tr
Radulaceae			
Radula antilleana Castle	1, 2, 3, 4	Br, Tr	Sh, Tr
R. frondescens Steph.	1, 2, 3, 4	Br, Tr	Sh, Tr
R. gottscheana Tayl.	1, 2, 4	Tr	Sh, Tr
R. javanica Gott. (= R. macrostachya Lindenb. & Gott.)	1	-	Tr
R. stenocalyx Mont.	3	-	Fo
R. tenera Mitt. ex Steph.	2	Br	-
Scapaniaceae			
Scapania portoricensis Gott.	4	Br (rare)	-
Trichocoleaceae			
Trichocolea flaccida (Spruce) Jack & Steph.	3		Fo
Trichocolea tomentosa (Sw.) Gott.	1, 2, 3, 4	Br	Sh, Tr

Cont. Table 1

	PLOT	CANOPY	UNDERSTORY
ANTHOCEROTAE			
Anthocerotaceae			
Megaceros vincentianus (Lehm. & Lindenb.) Steph.	4	-	Lo
MUSCI			
Bartramiaceae			
Leiomela bartramioides (Hook.) Par.	4	-	Tr
Brachytheciaceae			
Rhynchostegium serrulatum (Hedw.) Jaeg.	2	Br	-
Bryaceae			
Bryum capillare Hedw.	2	Br	-
Orthodontium pellucens (Hook.) B.S.G.	1	Br, Tr	-
Calymperaceae			
Syrrhopodon incompletus Schwaegr. var. berteroanus (Brid.) Reese	1, 2, 3, 4	Br (rare)	Trb
S. lycopodioides (Brid.) C.M.	4	Br	-
S. prolifer Schwaegr. var. tenuifolius (Sull.) Reese	4	-	Trb
Dicranaceae			
Campylopus arctocarpus (Hornsch.) Mitt.	1	Br	-
Holomitrium arboreum Mitt.	?	Br	-
Leucoloma cruegerianum (C.M.) Jaeg.	1, 2, 3	Br, Tw	-
L. serrulatum Brid.	1	-	Sh
Fissidentaceae			
Fissidens elegans Brid.	3	-	Trb
F. minutus Thwaites	1	-	Trb
F. steerei Grout	1	-	Trb
Hookeriaceae s.l.			
Callicostella pallida (Hornsch.) Aongstr.	1, 2	-	Lo
Crossomitrium patrisiae (Brid.) C. M.	2, 3		Fo
Daltonia gracilis Mitt.	1	Tw	-
Hookeriopsis falcata (Hook.) Jaeg.	1, 2, 3, 4	-	Lo, Trb
Hypnella cymbifolia (Hampe) Jaeg.	1, 2, 3, 4	-	Trb
H. diversifolia (Mitt.) Jaeg.	2	Br	-
Lepidopilum falcatulum C.M.	3	-	Sh
L. muelleri (Hampe) Mitt.	1, 2, 3, 4	-	Fo, Sh
L. scabrisetum (Schwaegr.) Steere	?	Br	-
Leskeodon andicola (Mitt.) Broth.	1, 3	-	Trb
L. cubensis (Mitt.) Thér.	3		Fo
Rhynchostegiopsis flexuosa (Sull.) C.M.	2	-	Lo
Hypnaceae			
Ectropothecium leptochaeton (Schwaegr.) Buck	2	Br	-
Mittenothamnium reptans (Hedw.) Card.	1, 4	Br	Lo
Hypopterygiaceae			
Hypopterygium tamariscinum (Hedw.) Brid.	2, 3	-	Trb
Leucobryaceae			
Leucobryum crispum C.M.	3	-	Trb
L. giganteum C.M.	1, 2	Br	-
Octoblepharum erectifolium Mitt.	4	-	Trb
Meteoriaceae			
Meteoridium remotifolium (C.M.) Manuel	2, 3	Br	Sh
Papillaria imponderosa (Tayl.) Broth.	2, 3	Br, Tw	Sh, Tr
Pilotrichella flexilis (Hedw.) Aongstr.	2	Br, Tw	-
P. pentasticha (Brid.) Wijk & Marg.	3	-	Tr
Squamidium nigricans (Hook.) Broth.	2	Br	-
Mniaceae			
Plagiomnium rhynchophorum (Hook.) T. Kop.	2, 3	-	Lo
Neckeraceae			
Isodrepanium lentulum (Wils.) Britt.	1, 4	Br	Sh
Neckeropsis disticha (Hedw.) Reichardt	1	-	Trb
Porotrichum korthalsianum (Dozy & Molk.) Mitt.	1, 2, 3, 4	-	Sh, Tr, Trb
P. longirostre (Hook.) Mitt.	2, 3	-	Sh
Porotrichum mutabile Hampe	?	Br	-
Orthotrichaceae			
Macromitrium cirrosum (Hedw.) Brid.	2	Br	-
M. mamillosum Bartr..	?	Br	-
M. cf. parvirete Bartr.	?	Br	-
M. cf. tonduzii Ren. & Card.	1, 2	Br	-
Phyllogoniaceae			
Phyllogonium fulgens (Hedw.) Brid.	2, 3, 4	Br	Sh (incl. var. gracile)
P. viscosum (P. Beauv.) Mitt.	1, 2, 3	Br	Sh
Prionodontaceae			
P. fusco-lutescens Hampe	2	Br	-
P. luteo-virens (Tayl.) Mitt.	3	-	Sh
Rhizogoniaceae			
Pyrrhobryum spiniforme (Hedw.) Mitt.	1, 2	Br	Lo
Rhizogonium lindigii (Hampe) Mitt.	1, 4	Br (rare)	Trb
Sematophyllaceae			
Acroporium pungens (Hedw.) Broth.	?	Br	-
Thuidiaceae			
Cyrtohypnum schistocalyx (C.M.) Buck & Crum	2, 3, 4	-	Lo, Trb
Thuidium antillarum Besch.	?	Br	-

Conventions

Br = thick, ± horizontal branches of the inner forest canopy
Fo = living leaves (foliicolous)
Lo = rotten logs
Sh = lianas, poles and small branches (of shrubs, treelets and saplings) in the forest understory
Tr = tree trunks (from 1 m upwards)
Trb = bases of tree trunks (0-1 m) and roots
Tw = twigs of the outer forest canopy

In a lowland rain forest of Guyana, Cornelissen and Gradstein (1990) found that about 50% of the bryophyte species were restricted to the canopy and 14% to the understory. The latter figures, however, were restricted to corticolous species and did not include species of rotten logs and living leaves. When calculations for the Monteverde study site are restricted to corticolous taxa, 52% of the species are exclusive to the canopy and 20% to the forest understory (Fig. 3B). It thus appears that the percentage of species restricted to the canopy may be the same in lowland and montane rain forests, in spite of the great differences in species abundance and composition in the two kinds of forest (see also Gradstein, 1995).

4. ***Floristics***. At least 19 species appeared to be previously unreported from Costa Rica (Gradstein et al., 1994): the hepatics *Adelanthus carabayensis*, *Bazzania affinis*, *Calypogeia crenulata*, *C. rhombifolia*, *Colura ulei*, *Cyclolejeunea accedens*, *Frullania exilis*, *F. laxiflora*, *Kurzia capillaris*, *Lophocolea connata*, *Marchesinia robusta*, *Metzgeria albinea*, *M. decipiens*, *Plagiochila rudischusteri*, *Prionolejeunea schlimiana*, *Radula antillana*, *R. frondescens*, *R. tenera*, and *Syzygiella pectiniformis*. Three of these, *Bazzania affinis*, *Lophocolea connata* and *Radula antillana*, were surprisingly common in the forest. Among the mosses and hornworts, none were new to the country.

The list includes several rare bryophyte species, known otherwise from only very few localities. *Plagiochila rudischusteri* is known from a few localities in northern Venezuela, Panama and Pacific Colombia, *Syzygiella pectiniformis* is a rare northern Andean species, and *Calypogeia rhynchophylla* is endemic to Costa Rican cloud forests with three known localities on the mainland and occurring also on Cocos Island, where it is very common (Dauphin, 1999). The rare endemic *Nowellia reedii* Robins., described from Monteverde (exact locality unknown) and not recorded anywhere else, was not found during this study.

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